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THE FLORAL ANATOMY OF THE URTICALES

ALBERT REIFF BECHTEL

(Received for publication February 9, 1921)

In the search for natural relationships in the seed plants, the morphologist and the anatomist have contributed much to the subject from work on the reproductive mechanism and on the structure of the vegetative organs. During recent years the breeder and the geneticist have presented theories based on experimental evidence which the taxonomist can not ignore. The subject of flower anatomy, however, has been limited in workers and in material studied. This subject should have contributions of value to offer for principles that are to be the guides in determining relationships within the angiosperms, as well as casting more light on the floral characters of the ancestors of the angiosperms.

There is as yet no definite knowledge of the ancestry of the various divisions of the angiosperms. Here hypotheses must be made from the study of external form upon which the classification has been mainly based, and these hypotheses must be strengthened or weakened by evidence from internal structure.

Different views have been held as to what the primitive flower was like. De Candolle (6) looked upon the primitive flower as hermaphroditic with all parts free. Engler (9) considered the simple, naked, unisexual flower as the primitive type. Bower proposed a bisexual flower with many sporophylls surrounded by one whorl of floral envelopes. The types of flowers known to us have been derived from ancestors, undoubtedly, like unto one or more of those above described, by the processes of amplification and reduction, which processes students of natural history accept as the great factors in molding our present forms of life.

Two cautions are suggested by Engler and Gilg (10) for students of phylogenetic relationships to heed: first, the consideration of a simple structure as primitive when it is reduced; second, the placing of reduced forms because of their reduction, too high in rank. There is a guide in this matter of interpreting reduced forms in Bower's (4) definitions:

Where the development of the natural organism, either in whole or in part, in external form or internal structure, falls short of that of the ancestry, that condition would be described as reduced.

Examples from among the earlier workers of the contribution of floral anatomy to the knowledge of the morphology and relationships of angiosperms are the following. In 1862, Darwin (5) declared the discovery of the nature of the orchid flower by studying transverse and longitudinal sections. His conclusions drawn at that time constitute our present interpretation

of the column and labellum. Gérard (11) in 1879 presented the anatomical features of numerous genera of the Orchidaceae. Upon Darwin's discovery it was at once suggested that the Orchidaceae are probably in the same line of descent with the Amaryllidaceae. In all characters the genera agree anatomically except in the androecium, which varies in position and in the number of the stamens and staminodes. Van Tieghem (20) in 1868 published the results of his extensive anatomical work on the flower, particularly on the structure of the pistil. This study treats of the various positions of the ovary with reference to other parts of the flower.

A search into flower anatomy should aid in revealing the following points: whether the same organs in different plants have taken on different functions; whether different organs perform the same function, or whether different forms of the same organ perform the same function (10); what is the condition of the vascular supply to aborted organs and to suppressed organs; whether any amplification in the floral organs has occurred; and what is the relative position of the floral organs, normal and abnormal.

The order Urticales, a study of which forms the subject of this paper, has been nearly universally accepted as a natural primitive order, but has been placed otherwise, bodily or in part, by the following students of taxonomy: Weddell (21), Lindley (13), Bessey (3), and Hallier (12). Although these students have not looked upon this order as among the very primitive angiosperms, they do agree that it belongs among the lower archichlamydeous forms. This study of the group is based upon the anatomy of the flowers and has as its object the possible determination of the phylogenetic position of this group so far as evidence may be offered by this field of research in conjunction with other parallel evidence.

Two treatments of the Urticales are in use to-day: that of Bentham and Hooker (2), which places all species in one family, the Urticaceae; and that of Engler (9), which divides the order into three families: Ulmaceae, Moraceae, and Urticaceae. For convenience in this paper the latter treatment is used.

The following characters possessed by this order of plants have caused them to be looked upon as primitive: flowers usually unisexual; floral envelopes composed of one whorl, which is generally spoken of as the calyx, and which is inconspicuous, bracteal, with parts similar and distinct or gamophyllous; stamens isostemonous; ovary superior, one-celled and one-ovuled, the ovule commonly orthotropous. In spite of these fairly primitive characters these plants have nevertheless been looked upon as somewhat reduced forms, the very features considered primitive being viewed as simple by reduction. The evidence from which such a conclusion is drawn is: apetalous and one whorl of stamens (Bessey, 3); a pistil with a unilocular ovary but with two styles, an indication of two fused carpels. Syncarpy is not considered primitive nor is the solitary ovule (3, 9); these are, on the contrary, the result of reduction. In the present paper are shown cases in

which the presence of one style in this order has prompted earlier students of taxonomy to infer the presence of but one carpel; internal anatomical study, however, reveals the unquestioned presence of two carpels.

MATERIAL

The flowers in this study were killed in chrom-acetic acid, embedded in paraffin in the usual way, and sectioned serially, the sections being eight and ten microns thick. Because the flowers are very small and ephemeral the vascular supply is very delicate and not readily differentiated. Experimentation with various stains proved the safranin and light green combination to be the most practical.

ULMACEAE

Ulmus. The species of this genus have flowers arranged in the inflorescence in a graded series from a short, slender, raceme-like cluster or a loose panicle-fascicle, with slender, jointed pedicels as in *Ulmus americana* and *U. racemosa*, to a very much reduced fascicle with pedicels practically eliminated as in *U. fulva*, *U. scabra*, and *U. campestris*. Taxonomists state, usually, that the flowers are simple with bell-shaped perianth, which is 9- to 4-lobed, imbricated, stamens opposite to, and of the same number as, the lobes, hypogynous, inserted at the base of the perianth; pistil of two carpels, each with a style, one loculus with a pendulous anatropous ovule.

The one-whorled perianth of *Ulmus* can be called neither sepaloid nor petaloid; it is succulent to membranous-scarious with little or no chlorophyll, possessing stomata equally distributed over its outer surface.

Ulmus americana L. has a flower (Pl. XV, fig. 1) which possesses a perianth of 8 lobes, three lateral right and three left, one posterior, and one anterior. Each lobe is accompanied by a stamen. Figure 1 shows the irregular character of the flower. This is a feature usually ignored. Lindley (13) mentions this condition; Britton, in his manual of the northeastern states and Canada describes it as "calyx oblique." This zygomorphy is evident in all the elms studied. Flowers sectioned in transverse planes from the pedicel to the distal end show that the vascular supply to the posterior organs usually passes off from the stele before that of the anterior organs. Such series of sections followed through numerous flowers of *U. americana* reveal the following facts.

The pedicel in all species of *Ulmus* has an ectophloic siphonostele in the form of a more or less continuous cylinder (Pl. XV, fig. 5). The first break in the stele is on the posterior side where a wide trace passes off leaving a gap in the cylinder. As nearly simultaneously with the break as can be appreciated, there separates from the inner face of this trace a portion composed of one or two vessels (fig. 6, *m*, *n*). The outer bundle is destined to pass to the posterior perianth lobe, and the inner to the accompanying stamen. Fifty microns above this section (fig. 6), the outer strand divides radially

into three strands (fig. 7, m), and fifty microns above the latter section these strands are well away from the stele and a second trace passes off lateral to the first (fig. 8, m^1) and behaves exactly like the posterior except for the subsequent branching. Twenty microns above the last section a trace, in appearance like the others, passes out of the stele opposite the second trace (Pl. XV, fig. 9, m^2); but twenty microns above this section, as represented in figure 9, the inner portion of this trace appears as a very faintly lignified vessel (figs. 10, 11, n^2), similar in origin and position to those supplying stamens with other lobes. This weak strand aborts seventy microns above its origin. It is clearly the supply to a suppressed stamen. The remaining lateral traces pass off right and left (Pl. XV, figs. 11–13) in close succession. The supplies to the anterior lobe and to the two anterior-lateral lobes appear to pass off simultaneously (Pl. XV, figs. 14–15, m^5 , m^6 , m^7), and all traces separate into staminal and perianth traces coincident with their departure from the stele. This fact is revealed also by longitudinal sections (Pl. XV, fig. 3, b).

When the strands to the perianth and to the stamens are definitely differentiated, such a distinct regional differentiation of tissue arises that the stamen supply is demarked from the adjacent tissues, forming what may be designated as a staminal cylinder (Pl. XVI, figs. 16, 17, c). This cylinder persists until the stamens become free from the perianth. At this level the branching of the perianth strands is usually complete; the posterior and anterior separate into two or three strands; the lateral strands rarely separate or branch (Pl. XVI, fig. 18, m , m^7).

With a knowledge of the gross morphology of the *U. americana* flower, the above described structure is really what might be expected. However, anatomical study reveals additional abortive bundles present in the anterior half of the flower. These bundles arise immediately within and above the bundles to the stamens and alternate with them. They appear in the same sequence as the bundles to the perianth parts and to the stamens and are evident in transverse sections as soon as the bundles to the stamens are distinctly established in the "cortical" region (Pl. XV, figs. 11–14, d^1 , d^2 . . . d^6 ; fig. 3, d^6 ; fig. 4, d^2 , d^3). These abortive bundles occurring above the bundles to the stamens and below the supply to the carpels show no lignification. They are characterized by cells of small size and by a tissue organization more close than that of the surrounding tissue. The origin of these strands from vascular bundles and the resemblance of the component cells to those of young or weakly developed bundles render their bundle nature undoubted. The centrally located cells of these demarked regions are very small and often exhibit the appearance of being crushed. They thus suggest the appearance of protoxylem as often seen in mature tissue. These abortive bundles extend upward approximately 150 microns. The question arises, are these the vestigial parts of suppressed stamens? There seems to be no alternative conclusion. The same phenomenon is found also with the strands leading to the carpels higher up in the floral axis (Pl. XVI, fig. 16, e ; Pl. XV, fig. 4, e) as discussed below.

Whenever the flower of *U. americana* has an equal number of perianth lobes and stamens, the number is usually 8 (Pl. XVI, fig. 22); occasionally 7, and rarely 9 parts occur in each whorl. In any case the suppression of an organ may occur. Figure 23 shows a flower with 7 perianth lobes and 6 stamens, and figure 24 shows one with 9 lobes and 9 stamens. The lowest number of lobes found in *U. americana* was 7 and the lowest number of stamens was 5.

Small lobes of the perianth frequently exist which are unobserved by means of the hand lens. These occur between and within two main lobes (Pl. XV, fig. 2, *a*). Anatomically, the vascular supply to this small lobe is a branch from a strand to a main lobe. However, there is a possibility that the strand to a main lobe is a union of two or three strands which originally passed to alternating parts of the perianth, and the branch to the small lobe may be the result of a separation of an aggregate strand rather than a case of true branching. Transverse sections frequently reveal indefinite organization of a perianth strand at its origin which may be due to the passing out together of several strands from the floral axis leaving a single gap.

An organized cylinder of vessels continues above the passing off of the traces to the perianth and to the stamens; this first suffers diminution, and then breaks into four strands. This latter change occurs before the stalk of the pistil is isolated from the tissue of the surrounding floral organs (Pl. XV, figs. 14, 15; Pl. XVI, figs. 16, 17). Two of these four strands pass up the posterior and anterior edges of the pistil respectively (Pl. XV, fig. 3, 1, 1¹; Pl. XVI, fig. 17, 1, 1¹) and are the dorsal carpellary bundles. The two remaining bundles, the lateral strands (Pl. XVI, fig. 17, *o*), bear towards the posterior side, approaching each other as they ascend and apparently forming one bundle (Pl. XVI, fig. 18, *o* + *o*). Serial sections (Pl. XV, fig. 15; Pl. XVI, figs. 16, 17, *o*) show that these strands in present development are apparently a continuation of the axis and not branches of the dorsal carpellary bundles (see discussion, p. 404). Where the pendulous ovule originates this composite strand separates into four strands, one passing into the ovule, one soon vanishing toward the posterior side of the pistil (Pl. XVI, fig. 19, *i*, *i*¹; Pl. XV, fig. 3, *i*, *i*¹), and two passing upward. The latter branch again sends bundles into the lateral edges of the two styles (Pl. XVI, figs. 19-21, *o*¹ and *o*²).

This separation of the ovule-bearing strand indicates the probability of the former presence of more than one ovule. The branching at the apex supplying both styles (Pl. XV, fig. 3, *o*¹, *o*²) indicates that these are the supply of an axillary placenta tissue. The existing ovule is in the anterior carpel. The aborted bundle (Pl. XVI, fig. 19, *i*¹; Pl. XV, fig. 3, *i*¹) is the remnant of the supply to the ovule that was borne in the posterior carpel and which still is present in some species (Engler, 9; Bentham and Hooker, 2; Baillon, 1).

Ulmus fulva Michx. is described as having perianth lobes and stamens ranging from 9 to 5. However, among the many flowers inspected by the writer, 8 was found to be the highest number and 5 the lowest, with one instance of the latter. The common number is 7 or 6, while in *U. americana* it is 8 or 7. The perianth of *U. fulva* is more prominently lobed than that of *U. americana*, but zygomorphy is as conspicuous. The traces to the floral organs pass off from the stele in close succession, but the traces to the stamens pass off higher up and later than do those to the perianth (Pl. XVII, fig. 1, *b*). *U. fulva* has abortive bundles similar to those of *U. americana*, alternating with the perianth and stamen strands. However, in this species these abortive bundles exist as a distinct whorl and not merely in the anterior part of the flower as in *U. americana*. These are organized tissues in the form of strands (Pl. XVII, fig. 2, *d*; fig. 1, *d*), but they possess no appreciable lignification. They persist to a level where the strands to the stamens are definitely isolated. The flower figured shows the anterior-lateral stamen suppressed, but its abortive trace (Pl. XVII, fig. 2, *s*¹) can be followed for 30 microns. The vascular supply to the carpels is the same as that of *U. americana*.

Ulmus racemosa Thomas is described as having the perianth lobes and stamens ranging from 8 to 5. All the flowers studied, from one tree only, had perianth lobes 8 to 7 and stamens 8 to 6. The flower tends to be zygomorphic to the same degree as that of *U. americana*. Traces into the floral organs originate and pass off in the same sequence (Pl. XVII, fig. 3, *b*; fig. 4). The presence of abortive bundles alternating with the bundles to the stamens and appearing later and above them was limited in this species to one instance (Pl. XVII, fig. 3, *d*, *d*¹). Here only two such bundles were found.

Ulmus campestris L. is described as having the perianth lobes and stamens varying from 5 to 3. In flowers from two trees, the perianth lobes were found to range from 6 to 4, and the stamens from 5 to 4; six lobes in the perianth are rare, and the common relationship is 5 to 4, or 4 to 4. The perianth cut away from the flower and studied under a microscope reveals the fact that the lobes are not the single structures that an observer takes them to be when inspecting the flower macroscopically. The hairy margin of the lobes obscures very small lobes on their sides (Pl. XVII, figs. 6, 7, *a*, *b*). In figures 6 and 7, the lobes 2 and 4 are anterior and posterior respectively; lobes 1 and 3 are lateral. Such is the origin and appearance, however, of these lateral veins *a* and *b*, that they should not be looked upon as branches of the midvein, but rather as veins separating from the vein leading to the main lobe. That is, veins *a*, 1, and *b* in figures 6 and 7 are the continuation of the traces, which pass out of the stele contiguously and remain in conjunction for a short distance, separating early. These bundles from their behavior (Pl. XVII, figs. 6, 7, *a*, 1, and *b*) may be considered alternating parts of two perianth whorls, which through reduction have

become consolidated except in their distal parts. Stronger evidence for the same conclusion is described for *U. americana* on page 390.

The vascular supply to the flower duplicates that of *U. fulva* (Pl. XVII, figs. 1, 2) and of *U. scabra* (Pl. XVII, figs. 8-10). Commonly one and sometimes two perianth lobes have the stamen suppressed even in the vascular supply.

Ulmus scabra Mill. is described as having the perianth lobes and stamens ranging from 6 to 5; a study of many flowers reveals that 6 perianth lobes and 6 stamens appear in the majority of cases. The vascular supply to the perianth and to the stamens arises separately (Pl. XVII, fig. 8, *b*) as it does in *U. fulva* and in *U. campestris*. The strands to the perianth lobes (Pl. XVII, fig. 9, *m* . . . *m*⁵) are well out in the "cortical" regions when the supply to the stamens is just passing out of the stele (fig. 2, *n* . . . *n*⁵).

U. scabra presents a feature not found in any of the other species. Alternating with the traces to the perianth lobes and arising with them are bundles that apparently lag behind (Pl. XVII, figs. 9, 10, *x*, *x*¹, *x*²; fig. 8, *x*, *x*²; Pl. XVIII, figs. 1, 2, *x*, *x*¹, *x*²). These are perianth bundles but they always continue inside the strands to the perianth lobes. They do not have the number of lignified cells, nor the size of cells that the strands to the perianth lobes possess. They weaken rapidly and vanish on a level with the origin of the lobes of the perianth. Such bundles were not found in the posterior part of the flower (Pl. XVII, fig. 9). The anterior part of the flower of *Ulmus* is clearly the conservative part of the flower, since in this part the stamens opposite the perianth lobes are always present. Suppressed stamens occur in the posterior part of the flower, or here the stamen is present and the perianth lobe is suppressed. Also, the abortive bundles described in the above named species usually occur in the anterior part of the flower except in *U. fulva* where they make one complete whorl (Pl. XVII, fig. 2, *d*), but the abortive stamen, *s*¹, in the same figure, is in the posterior part of the flower. Thus, as described above, *U. scabra* presents an additional feature in the anterior part of the flower, namely, the weak bundles to the perianth lobes. These bundles, *x*, *x*¹, *x*², may be vestigial parts of suppressed perianth parts which alternated with the present perianth lobes. The origin, the position, and the appearance of these weak bundles offer no other disposition except that of a vascular supply to corolla parts which have been reduced and consolidated in the gamophyllous perianth.

Alternating with the strands of the perianth, except with the posterior strand, are organized tissue regions as in the other species suggesting bundles, but these show no lignification (Pl. XVII, fig. 9, *d*). The same condition has been fully discussed above in the other species. Again, there seems to be no other alternative here than to look upon these as abortive bundles to a suppressed outer whorl of stamens.

The carpel supply duplicates that of the above named species. Figures 9 and 10 in Plate XVII and figures 1 and 2 in Plate XVIII are from a flower with three carpels developed. This may be looked upon as an abnormality, yet this extra carpel is a character parallel with the seven aborted bundles (Pl. XVII, fig. 9, *d*) alternating with the perianth traces instead of the five or three abortive bundles in flowers which have the usual two carpels. This flower has also three abortive bundles in the perianth (Pl. XVII, figs. 9, 10; Pl. XVIII, figs. 1, 2, *x*, *x*¹, *x*²) which have been considered above as petal traces instead of two or no such traces in the bicarpellate flower.

Celtis occidentalis L. reveals a symmetry of 6 or 5; any other rarely occurs. A unique flower was found with seven perianth lobes and five stamens. This was selected to figure on Plate XVIII. The pedicel as it passes into the flower presents a stele that organizes itself into anterior and posterior sections (Pl. XVIII, figs. 4-6). From both of these sections bulky strands pass out, and each of the latter separates into two strands passing to the perianth lobe and to the stamen respectively (fig. 3, *b*; figs. 6, 7, *m*, *n*). This common origin of the vascular supply of the perianth and stamens and the persistence of this condition for a short distance is a new feature in the Ulmaceae. In addition to this is the unusual origin of the ovule supply. This arises distinctly from the dorsal carpellary strand of the anterior carpel and passes towards the posterior side of the pistil upward into the pendulous ovule (figs. 3, 8-11, *o*). The two lateral strands (figs. 9-12, *o*¹, *o*²) pass up separately and vanish at the base of the styles. The course of these lateral strands is very different from that of the lateral strands in the *Ulmus* pistil where the lateral strands approach and join to form the ovule supply (Pl. XVI, figs. 17, 18, *o*). Also branches from the ovule-bearing strands in *Ulmus* continue in the inner lateral edges of the styles, but in *Celtis* there are no branches from the ovule-bearing strand. In this respect the ovule-bearing strand of *Celtis* is similar to that of the remaining species of the Urticales studied. The lateral strands of the pistil of *Ulmus* are, therefore, not homologous with those of the pistil of *Celtis* although they apparently originate in the same manner. In *Ulmus* they are the placental supply, but in *Celtis* they may be regarded as abortive, dorsal, carpellary bundles of suppressed carpels. The placental supply in *Celtis* arises distinctly from the anterior carpel supply. Evidently reduction in the gynoecium of *Ulmus* has proceeded to a much greater degree than in *Celtis*. In *Ulmus* the placental supply has apparently lost connection with the carpel supply and arises from the axis of the flower (see discussion, p. 404).

The staminate flower of *Celtis* possesses an abortive pistil, a miniature of the pistil in the hermaphroditic flower, except that the lateral bundles in the pistil (figs. 9-12, *o*¹, and *o*² above) are not present. The dorsal carpellary bundles of the abortive pistil continue into the two styles. The posterior style is smaller and less succulent than the anterior style. Here is

a consistency in abortion, the posterior carpel being the sterile carpel in the hermaphroditic flower and the more greatly reduced carpel in the staminate flower; and the lateral strands of the pistillate flower (figs. 9-12, σ^1 and σ^2), regarded as dorsal strands of abortive carpels, are suppressed in the abortive pistil of the staminate flower.

MORACEAE

In brief, the plants of this family are woody with small flowers usually in dense clusters, unisexual; the perianth 5- to 4-parted, stamens equal in number with, and opposite to, the parts of the perianth; ovary one-celled with single pendulous ovule, styles 2 or 1. The ovule is "basal" (1, 9) in a few species.

Morus alba L. presents in the pedicel of the pistillate flower a stele of four traces (Pl. XIX, figs. 2, 3). From these four traces pass off in a decussate manner the posterior and anterior traces, followed closely by the lateral (fig. 4, p , p^1). These traces supply the four perianth parts, and in each part the bundle separates into three strands (figs. 4, 5, p , p^1). The floral axis above the point of departure of the perianth traces continues as four strands, posterior, anterior, and two lateral. The anterior and posterior strands are the dorsal bundles of the two carpels (Pl. XIX, figs. 4-9, 1, 1¹) and pass on into the styles. The two lateral strands, as in *Ulmus*, approach each other as they ascend, unite, and pass upward into the ovule (Pl. XIX, figs. 1, 4-7, σ). In *Morus alba* these two strands to the ovule do not receive any evident vascular supply from the anterior carpellary strand as figured by Welsford and Benson (22) for *M. nigra*.

The pedicel of the staminate flower (Pl. XIX, fig. 10) shows many strands in the stele which organize into four strands in the base of the flower. From these, four traces pass off decussately and each soon separates into strands to the perianth parts and to the stamens. The dorsal carpellary supplies persist in the abortive pistil of the staminate flower (Pl. XIX, fig. 10, 1, 1¹).

An interesting difference in the vascular supply to the perianth parts of the pistillate and staminate flowers is that there are three traces to each part in the former and only one in the latter. In the pistillate flower, the perianth persists in the fruit as a fleshy organ and calls for a vigorous vascular supply. The staminate flower functions to the time of pollen production and then falls. As a result, the vascular supply to its perianth has degenerated to a single weak strand in each lobe. This is an illustration of what happens frequently in members of the Urticales. The organ degenerates to the extent that the apparent demand for it decreases.

Maclura pomifera (Raf.) Schneider has its pistillate inflorescence in a dense, succulent head, the individual flowers being sessile. A transverse section of the inflorescence axis below the bases of the flowers shows the many pedicellar steles surrounded by a continuous, extremely delicate,

parenchymatous tissue. Each stele is composed of four strands. From these strands there pass off in the base of the flower four traces to the perianth (Pl. XIX, figs. 11, 12, *p*); the remaining four continue into the pistil (figs. 11, 12, 1, 1¹, *o*). The perianth parts become distinct at a level with the ovule (fig. 16), which is not far above the level where the flowers become distinct from each other (fig. 13).

The perianth parts vary much in the amount of vascular supply. In addition to the one main bundle, there frequently exist in the same inflorescence flowers having perianth parts with few to many small, weak bundles (Pl. XIX, figs. 14-17, *n*). The peculiar feature of these bundles is that they cannot be followed to their origin because of the lack of any organization suggesting bundles in the lower part of the perianth. These small strands are either branches of the main bundle of the perianth part, or, as shown in *Ulmus*, they are a separation of the strands that are now passing off from the floral axis as a common trace. The presence and abundance of these faint bundles vary according to the crowding of the flowers in the dense capitate inflorescence. The two lateral strands to the pistil (Pl. XIX, fig. 12, *o*) approach each other, becoming one strand (figs. 13-16, *o* + *o*) which passes to the posterior side upward into the pendulous ovule (fig. 18, *o*). The anterior bundle passes up the anterior side of the pistil to the tip of the single filiform style. This is the bundle to the anterior carpel (figs. 12-18, 1). The corresponding bundle passes up three-fourths of the height of the ovary (figs. 12-18, 1¹), on its posterior side. Comparing the vascular supply of the two carpels of *Morus* with that of *Maclura*, the conclusion is that the posterior carpel of *Maclura* is abortive. This abortion of the carpel and the non-actinomorphic condition of the flower make zygomorphy a feature of the *Maclura* flower.

In the staminate flower four traces from the pedicel separate into strands to the perianth parts and to the stamens. The carpels are suppressed, and there are no signs of any vascular tissue in the central portion of the flower (Pl. XIX, fig. 19).

Cannabis sativa L. The pedicel of the pistillate flower has four stelar strands (Pl. XX, fig. 2). One of these strands (fig. 2, *a*) passes off anteriorly into the bract which completely envelops the flower (figs. 2-4, *br*). The three remaining strands pass up into the pistil of the flower. Two strands (Pl. XX, figs. 2, 3, 1, 1¹) which have nearly the same size pass up the dorsal sides of the two carpels to the tips of the two styles respectively (figs. 2-8, 1, 1¹). The fourth strand of the pedicel, which is opposite the strand passing into the enveloping bract, is twice the size of any of the other strands (Pl. XX, figs. 2-4, *o*). This strand maintains its bulkiness as it passes up posteriorly into the pendulous ovule (figs. 5-7, *o*).

A transverse section of the flower just below the ovule shows six distinctly lignified bundles in the perianth (Pl. XX, fig. 5, *m*). The appearance of the tissues of the perianth suggests more bundles than those having

vessels. None of the bundles, even those with lignified cells in their upper portions, can be followed to their origin in the floral axis. The posterior bundle (fig. 4, *m*) can be followed down the farthest, that is, into the cortex of the pedicel or receptacle. It does appear that the perianth bundles are abortive in the lowest part of their courses.

Payer (14) and Zinger (24) describe and figure the cup-like perianth as having slightly developed anterior and posterior lobes. Anatomically, the author found no difference in the lobed regions as compared with the remainder of the perianth except the fact that the most prominent bundle to the perianth is the posterior bundle.

A feature of the pedicellar stele not yet described is the presence of regions suggestive of bundles (Pl. XX, figs. 3, 4, *x*). Such a condition described in the preceding species was looked upon as one demonstrating abortive bundles. Such faint bundles and others not recognizable may pass into the perianth and become lignified in their upper parts only, a condition such that they can be followed. Also in the upper lateral ovary wall there are faint bundles with delicate, lignified cells (Pl. XX, fig. 5, *n*) which cannot be followed to their origin. These must be either branches of the dorsal carpellary bundles or strands continuing from the pedicel. If the latter, they arise similarly to the two dorsal carpellary bundles and therefore suggest abortive carpellary bundles to suppressed carpels.

The stele in the pedicel of the staminate flower is very different. It has many small strands which organize into five strands in the base of the flower. These pass out of the axis and each separates immediately into strands to the perianth and to the stamens. There are no signs of abortive strands to the suppressed carpels in the writer's experience. Likewise in the pistillate flower, the stamens are suppressed and no vestiges of vascular supply are present.

Pritchard (16) concludes from his experiments on the hemp plant that both the male and the female flowers are potentially hermaphroditic and that the unisexual condition is the result not of different zygotic constitution, but of the lack of food supply. At what time in the life of the hemp plant the suggested feeding must be begun in order to establish organs that are suppressed, even in vascular supply, is an interesting problem to a plant anatomist. It may indicate that the unisexual nature of the hemp flower is not well established. Some of its congeners in the order still have bisexual flowers.

Humulus Lupulus L. The pedicel of the pistillate flower duplicates in structure that of *Cannabis* except that it has fewer vessels in each of its four bundles. Anteriorly, a large trace passes out and branches profusely in a large bract which envelops the flower (Pl. XX, fig. 9, *br*; fig. 10, *a*). The three remaining strands in the pedicel, as in *Cannabis*, pass into the pistil. Strands (figs. 14-18, 1, 1¹) pass up the dorsal sides of the two carpels into the styles respectively. These are the dorsal carpellary bundles. The

remaining strand (figs. 9, 14-16, *o*) passes up posteriorly into the pendulous ovule. The pedicel of *Humulus*, also, possesses in its upper portion definitely organized tissues suggesting bundles (figs. 10, 11, *x*). One of these suggestive regions does possess a faintly lignified vessel (fig. 10, *x*) which must eliminate all doubt of its being a bundle.

The perianth of *Humulus* is very similar to that of *Cannabis sativa*. Transverse sections through the upper part of the perianth reveal many bundles (Pl. XX, fig. 16, *p*), varying in number from 10 to 14. These bundles cannot be traced to an origin in the pedicellar stele, but they can be followed passing into the cortex. Figures 12, 13, 14, and 15 show the traces to the perianth numbered in the order in which they become distinguishable, *e.g.*, figs. 12, 13, 1¹, 1², 1³. Because of the delicate cell walls, it cannot be definitely said whether there are three, five, or more original traces leading into the perianth. However, it is evident that several traces to the perianth originate at one point in the stele, or that the traces separate after they passed out as one trace (figs. 13-15). Since the perianth strands are difficult to trace owing to their delicacy, we conclude, as for *Cannabis*, that the basal portions are abortive.

In *Humulus*, as in *Cannabis*, the abortive bundles in the pedicel may continue into the perianth and show lignification only in their upper portions. A fact supporting this conclusion is that these abortive bundles appear after the strand to the bract is oriented and before the appearance of the remaining strands that pass into the pistil. In all other species studied in the Urticales, the perianth bundles pass off first or lowest on the floral axis, and this is the position of the abortive bundles of *Humulus* and *Cannabis*.

URTICACEAE

This family of the Urticaceae contains perennial or annual herbs with very small, greenish flowers, monoecious, dioecious, or polygamous; perianth parts 5 to 2, distinct, cleft, or tubular; stamens of the same number and opposite to the perianth parts; ovary with one cell, one "orthotropous" ovule; styles usually capitate and sessile.

Urtica gracilis Ait. is figured in Plate XXI. The vascular supply in the minute pedicel of the pistillate flower appears as one strand (fig. 2) which gives off two decussate pairs of bundles which pass to the four perianth parts (figs. 3-12, *m*, *n*). The remaining vascular tissue continues as four strands into the pistil. The posterior strand passes up into the sessile stigma. This strand is the dorsal carpellary bundle of the posterior carpel. The anterior strand passes up three fourths of the height of the ovary and cannot be followed further. The two lateral strands approach each other as they ascend and enter the funiculus of the basal ovule as one strand (figs. 1, 5-11, *o + o*), as was found in *Ulmus*, *Morus*, and *Maclura*. In interpreting the vascular supply of this pistil similarly to that of *Ulmus* and others previously described, the conclusion is that two carpels are present

but that the anterior carpel is partially abortive. However, *Urtica* has been looked upon as being "unicarpellary" (Baillon, 1; Bessey, 3).

Transverse sections of the *Urtica* flower indicate zygomorphy: the two lateral perianth parts are alike; but the posterior is larger than the anterior and is the last to become distinct from the shallow perianth tube (figs. 1, 10-13, *m*); the pistil does not stand in the middle of the flower.

Boehmeria cylindrica L. (Sw.) possesses a tubular flower with the vascular supply of the perianth confined to the anterior and posterior sides (Pl. XXII, figs. 1, 3-7, *m*). This fact indicates that the lateral perianth parts have been consolidated with the anterior and posterior parts and that their vascular supplies have completely degenerated. This flower shows the zygomorphic features of the *Urticales*.

Only two strands pass into the pistil instead of four as in *Urtica gracilis*. These two strands arise from one strand (Pl. XXII, figs. 3, 4, 1¹ and *o*) in the basal portion of the flower. The posterior strand passes up the posterior side of the pistil into the short filiform style and is the dorsal carpellary bundle. The other strand ascends anteriorly for a short distance and then sharply curves towards the posterior; after passing horizontally in this direction for a short distance it abruptly ascends into the "basal" ovule (figs. 1, 5, *o*). The anterior side of the pistil has no vascular supply. Here undoubtedly the anterior carpel is suppressed. Therefore, *Boehmeria cylindrica* has reached that stage in reduction having only two perianth parts, one carpel, and a "basal" ovule. The ovule from the path of its bundle (fig. 1, *o*) indicates that its apparent orthotropous nature has become such by a sinking down to a basal position from a pendulous or lateral position.

In the base of the staminate flower, the strands of the pedicel conjoin (Pl. XXII, figs. 9, 10, 11) and strands then pass off to the perianth and to the stamens (figs. 9, 12, *m*, *s*). The staminate flowers have an abortive pistil which possesses a weak vascular supply (figs. 9, 12, 1, 1¹).

Laportea canadensis (L.) Gaud. has a flower that is decidedly zygomorphic. The floral structures vary from those described above. The anterior perianth part is large, the posterior is very small, and the lateral parts are alike. From a cylindrical stele (Pl. XXII, fig. 15) of the tiny pedicel a strand passes anteriorly into the anterior perianth part (figs. 14, 16, *m*). No strand corresponding to the anterior perianth strand passes off into the small posterior perianth part (figs. 14, 16, *m*¹). Two strands pass off laterally to the lateral perianth parts. Evidently the decussate arrangement of the perianth supply as exhibited in *Urtica gracilis* is broken in *Laportea canadensis* through the suppression of the posterior perianth trace, although a very small perianth part is still present (figs. 14-19, *m*¹).

Above the origin of the perianth bundles only two bundles continue, and these in an anterior-posterior plane. The posterior bundle passes up the posterior side of the pistil into the single style (Pl. XXII, figs. 14, 16-21,

1¹). The anterior bundle (figs. 14, 16, 17, *o* + 1) continues for some distance and then separates into two unequal strands, one passing into the anterior side of the pistil and the other, the larger, passing into the ovule (figs. 14, 18–20, *o*, 1). The former strand soon vanishes in the lower third of the ovary wall (fig. 14, 1). This is evidence of an abortive anterior carpel.

The ovule and its vascular supply again offer opportunity for speculation. After the anterior carpel strand separates from the single anterior strand, the main supply passes horizontally in an ascending-posterior direction through a long stocky funiculus into the ovule (figs. 14, 18–20, *f*, *o*). The position of the ovule suggests the reduction of an axillary placenta which bore ovules in a pendulous position. The ovule is past the midway stage between that of a pendulous ovule as in *Ulmaceae* and *Moraceae* and that of a basal ovule as in *Boehmeria cylindrica*. In fact, very little reduction in funicular tissue in *Laportea canadensis* is necessary to duplicate in position that of the ovule of *Boehmeria* (compare Pl. XXII, figs. 1 and 14). The same line of reasoning is suggested upon comparing the ovule supply of *Boehmeria cylindrica* and *Urtica gracilis* (Pl. XXI, fig. 1; Pl. XXII, fig. 1), namely: the bundle in its indirect route to the basal ovule of *Boehmeria* would require little reduction to duplicate the direct supply to the basal ovule of *Urtica*.

DISCUSSION

Ulmaceae. The gross floral morphology of the six species and the detailed anatomy underlying it have been presented above. The latter reveals features which warrant the disuse of the descriptive term "simple" for the flowers: five sets of organs or vestiges of organs; variableness in number of parts in a whorl; zygomorphy, which is constant; and the fusion of like and unlike parts. These present a decidedly complex condition.

The flowers of the genus *Ulmus* have a perianth "cup" upon the edge of which the perianth parts and stamens have been considered perigynously inserted. Baillon (1) considered this to be the condition. Anatomical work reveals that this is not the case for the following reasons. First, the vascular supply to the stamens and to the perianth parts arises separately from the stele of the pedicel; the former passes off from the floral axis considerably above that to the latter in *U. fulva*, *U. campestris*, and *U. scabra* (Pl. XVII, figs. 1, 5, 8, *b*), but approximately closely in *U. americana* and *U. racemosa* (Pl. XV, fig. 3; Pl. XVII, fig. 3, *b*). Second, the tissues embodying the perianth and stamen traces through the perianth "cup" are separable by the distinct difference in cellular structure and by a line of demarcation. These differences in the parenchymatous tissue are collateral and continue into the perianth lobe and stamen respectively. The line of demarcation indicates an adnation of the tissues of the perianth lobe and stamen. Here is good evidence that the "cup" is the fused bases of floral envelopes and stamens. Third, the lobes of the perianth are variable in length; their size is not constant, which is a character not un-

common in hypogynous flowers. The last is among the characters used by Planchon (15) in distributing the 16 species of *Ulmus* into three divisions.

Celtis has perianth parts distinct to the base or nearly so. The remaining genera of the Ulmaceae, eleven in number, have perianth parts similar to those of *Celtis* (2). In the Ulmaceae the receptacle is limited, then, to the pedicel of the flower, and in *Ulmus*, coalescence and adnation have taken place in the perianth parts and stamens. Also, the fact that the single whorl of normal vascular bundles to the perianth and to the stamens, respectively, is accompanied by whorls of abortive bundles which alternate apparently with these, enforces the conclusion that along with the coalescence and adnation, there has been reduction in these two sets of organs. This reduction consists of the loss of an inner whorl in each. Reduction occurs not only in the number of whorls but also in the number of organs within a whorl. No constant number exists in the floral whorls of any of the elms. Greater variation occurs in those species having the greatest number of organs present per whorl; *e.g.*, in *U. americana*, as described on page 390, there are 9 to 7 perianth lobes and 9 to 5 stamens. The cause of the lack of floral symmetry in a species is due to the development of a perianth lobe without its accompanying stamen. This is usually the stamen to one or the other of the posterior-lateral lobes. However, just as often, a stamen develops without an accompanying perianth lobe. The number ranges from 9 in *Ulmus americana* to 4 in *U. campestris*, and is more or less inconstant in all species. On the basis of inflorescence (which shows in *Ulmus* stages in reduction), the species with more floral parts are more primitive than those with fewer. Although the gynoeceium of Ulmaceae is dimerous, from the presence of abortive strands to suppressed carpels it has suffered reduction. Such organized tissue regions suggesting bundles were discovered in *Ulmus americana*. These bundles appear some distance above those to the stamens, on a level from which the strands to the carpels can be followed.

Ulmus possesses spirally arranged parts (Pl. XV, figs. 7-14), though the other genera studied are cyclic. The spiral arrangement is most conspicuous in the species with the greatest numbers of stamens and perianth parts and becomes less conspicuous in those elms in which the floral characters grade into those of the Moraceae which are tetramerous and cyclic. The spiral arrangement is an important phyletic character, but by reduction in the number of organs and in the floral axis, it has become nearly obscure.

The alterations in the posterior part of the flower over those of the anterior part by modification in the relation of organs to each other, and by the suppression of organs, form a true zygomorphy. This character is perhaps the result of aggregation (23), and possibly an adaptation to insect visitation. To be sure, very few species in the Urticales are known to be visited by insects, yet zygomorphism may be a character persisting from an earlier time when insect visitation was the common occurrence. There is a possibility that zygomorphism as a specialized character and as a character

particularly adapted to insect visitation has been over-emphasized. Evidence has been presented that the angiospermous prototype (Robertson, 17) was entomophilous and that the anemophilous condition has been recently acquired. A character that in many instances accompanies the entomophilous flower is the multiovulate condition. The vascular supply of the placenta of *Ulmus*, the flowers of which are least reduced of those genera studied, indicates that whereas but one ovule is now borne, a multi-ovulate condition probably existed formerly.

The characters gamophylly, zygomorphy, bicarpellate, uniovulate ovary, vestigial organs, indicate certain specialization and a high flower type. However, it is only in *Ulmus* that the gamophyllous character exists. The gamophylly of *Ulmus* is to be considered an isolated instance of this tendency in the Polypetalae. Finally, from the evidence gathered, the Ulmaceae are primitive forms but with many advanced characters. They should be considered highly reduced and specialized forms among primitive groups.

Moraceae. The flowers of *Morus* and *Maclura* are anatomically alike, although the former has a pistil with two styles and the latter a pistil with one style. Anatomy reveals two carpels in each case. This reduction in the gynoecium of *Maclura* is no doubt a feature accompanying the dense inflorescence. For the same reason the common variation in the size and venation of its perianth parts, as previously described, occurs. The three-veined character of the perianth parts is constant in the *Morus* pistillate flower but not constant in that of *Maclura*. This suggests a palmate venation which corresponds to the venation of the foliage leaves. The leaves of *Morus*, as in many related genera, have three basal veins, and when the foliage leaves are large they have three lobes. According to Sinnott and Bailey (19), palmate venation is the primitive type in the angiosperms, and where it occurs in the floral parts only, as it does inconstantly in *Maclura*, it is a "persistence of an ancient character which has been lost elsewhere." This sign of primitiveness is conspicuous also in the perianth parts of *Ulmus* (p. 388). The anterior and posterior perianth parts have three veins as a nearly constant character. The midvein departs first, and soon the lateral veins separate from it.

Humulus and *Cannabis* form a type distinct from *Morus* and *Maclura*. The very delicate gamophyllous perianth in the pistillate flowers (p. 396) has been produced undoubtedly by the large persisting bract which envelops these flowers. Since the vascular supply is evident only in the upper part of the perianth, it is an indication that the perianth is in the process of disappearing. As the venation in the perianth parts of *Ulmus* and *Morus* was interpreted by referring to the venation of the foliage of the same, the perianth of *Humulus* and *Cannabis* can be so interpreted. The leaves of these two species have palmate venation and both are multi-digitately veined. Thus the many small veins of the perianth of *Humulus* and *Can-*

nabis, the origin of which cannot be determined in the gamophyllous perianth cup, may be considered veins of several digitately veined perianth parts. They attain a weak development due to reduction. The floral envelopes have become reduced and delicate with the development of a large protecting bract. The differences in the ovule supply in these genera will be elaborated upon in the general discussion (p. 404).

Thus, the flowers of the Moraceae as compared with those of the Ulmaceae have been more greatly reduced in floral axis, as described earlier in this paper, in perianth lobes, and in their vascular supply, as seen in *Maclura*, *Humulus*, and *Cannabis*, and in the gynoeceum as illustrated in *Maclura*.

Urticaceae. The study of three species of this family indicates the presence of that reduction which is found in its earlier stages in Moraceae, namely, the suppression of one of two carpels. In *Urtica* and in *Laportea* the anterior carpel is represented only by abortive bundles; in *Boehmeria* there is no trace of a bundle in this carpel. Also the irregularity of the perianth parts is slight in *Urtica*; it is greater in *Laportea* to the degree that the posterior perianth part has nearly disappeared, and has no vascular supply. In *Boehmeria*, an anatomical study of the gamophyllous perianth reveals two perianth parts only. There is no evidence of lobes indicating lateral perianth parts, nor bundle supply to such parts. The "orthotropic" ovule supply, as has been presented on page 398, gives evidence by its peculiar course of a change of position of the ovule from a pendulous or lateral to a basal position. The irregularity of the shape and size of the perianth parts, the number of parts, ranging from four to two, the "basal" ovule supplied by a bundle taking an ascending and then a descending course, indicate a reduction in this family beyond that found in the Moraceae.

Along with the floral reduction in the Urticaceae goes the herbaceous perennial or annual plant habit which character phyletically (7, 18) is in keeping with that of the flower.

GENERAL DISCUSSION

The Urticales present an anomalous combination of characters. These on one hand indicate primitiveness and on the other specialization. Many and indefinite organs, non-cyclic condition, preponderance of woody forms, and palmate venation, still evident in the perianth parts if not in foliage leaves, point to primitiveness. Aggregation of flowers, fusion of parts, zygomorphy, and reduction point to specialization. Therefore, they must be considered at least not highly advanced forms, though they possess a number of very advanced features. Almost any group of angiosperms possesses one or more of the characters indicating high rank. The presence of several such characters in the Urticales is not an indication of particular

advance over other groups. Nor is the presence of zygomorphism, for example, an indication of relationship with another group in which the same feature is present. That the Urticales are related to one of those plexuses of the angiosperms possessing types of zygomorphism, namely: that culminating in the Monocotyledons, that of the Rosales in the Polypetalae, and that of the Tubiflorae in the Sympetalae, can receive no support. It does seem that a relationship more nearly correct may be discovered for the Urticales by considering the characters possessed by them that indicate primitiveness rather than those that indicate specialization, namely: many organs, non-cyclic conditions, and preponderance of woody forms. The one order of the angiosperms possessing these characters is the Ranales. The Ranales have not suffered reduction to any degree comparable with that of the Urticales. Floral anatomy of the members of the families of the Ranales may reveal important characters that macroscopic study cannot reach. However, the Urticales appear, when viewed from the standpoint of their primitive characters, to be parallel with the Ranales. The latter possesses a tendency to the pentamerous condition, and both orders possess a tendency to an unicarpellate condition. That the Urticales and Ranales are descendants from the same protoangiospermous plexus seems likely. But, since the flowers of the Urticales are greatly reduced in each set of organs, as the floral anatomy described above indicates, the Urticales are on a higher level than the Ranales.

A feature of the Urticales that has caused them to be looked upon as very primitive plants among the angiosperms is the "orthotropous" ovule. This type of ovule has been regarded as the most primitive since it is apparently the common type appearing in those families classified as lowest in the Polypetalae. In the most highly reduced members of the Urticales, numbering about half the species of the order, the ovule is "basal" or "orthotropous." Anatomical work reveals, however, that the ovule has become basal, as previously described, by a sinking or a sliding down from a pendulous position and that in this process the anatropous ovule has become erect. Thus the Urticaceae show a phyletic origin of the orthotropous ovule from an anatropous, pendulous, or lateral type, as Welsford and Benson (22) consider is the case in *Juglans regia* and related plants, basing their evidence also on anatomical study. The orthotropous ovule in this group, therefore, is not primitive. The floral anatomy of Bentham's Incompletae (15 orders), in which the ovule, with few exceptions, is basal, is an inviting line of research. In determining the phyletic relationship of the Urticales, therefore, it is the pendulous or lateral anatropous ovule that must be considered and not the erect basal ovule.

A consideration of the vascular supply to the ovule, as described in the species studied, may indicate that the Urticales are not a natural order. Three types of vascular supply to the ovule were found, but these are all the results of the greatly reduced condition of the flowers. The common

type, as found in *Ulmus*, *Morus*, *Maclura*, and *Urtica*, representatives of the three families of the order, is an ovule supply which is the result of the fusion of two lateral strands from the floral axis. The second type is found in *Celtis* and in *Laportea*, where the ovule supply is a branch from the anterior carpellary strand. The third type is in *Humulus* and in *Cannabis*, where the ovule supply is a continuation of a single strand from the pedicel.

The first two suggest a foliar origin for the ovules. The two lateral strands passing to the ovule are two lateral basal veins arising with the midvein of the anterior carpel. This condition strongly suggests the carpel to be a foliar organ with palmate venation. Possibly the ancestral condition was that of a carpel with several ovules, two at least, one borne on each of these basal lateral veins; but through coalescence and reduction the two veins conjoined and one ovule was crowded out. It is likely that other lateral veins of the dorsal carpellary bundle above the two existing bearing ovules have disappeared through the same processes. The same thing seems to have happened in the posterior carpel of *Ulmus*. An abortive ovulary branch of the placental strand, in which are incorporated the abortive lateral strands (basal veins) in the anterior and posterior carpels, is present just opposite the branch passing into the ovule (Pl. XVI, fig. 19, *i*¹; Pl. I, fig. 3, *i*¹). The ovule belonging with this strand is occasionally present in *Ulmus* and in *Morus* (Baillon, 1; Engler, 9). The strand leading to the ovule in *Humulus* and in *Cannabis* arises deep in the pedicel. It is posterior and opposite to the strand that passes into the enveloping bract (Pl. XX, fig. 2, *o*, *a*), and is the largest of the four strands in the pedicel. The single pedicellar strand to the ovule and the phenomenon present there are due undoubtedly to the greatly reduced state of the flowers, described previously (p. 402), which has altered the ovule supply to a single strand. In the anterior carpel the lateral carpellary veins have disappeared and the midrib is small, undoubtedly because of the development of the large bract. The same bundles in the posterior carpel have fused into one strand passing to the single ovule. The ovule and the ovule supply, therefore, indicate a natural order for the *Ulmaceae*, *Moraceae*, and *Urticaceae*. When the ovule of the *Urticales* is taken into consideration to determine the likely relationship of the order, the type of ovule as found in *Ulmaceae* must be used. That type is the anatropous, pendulous, or lateral ovule, which is the primitive type in the *Urticales*. The partial basal or basal-erect ovules are the result of reduction as the comparative anatomical studies previously described indicate.

The accepted relationship of these three families on the part of taxonomists is supported by this study of floral anatomy. The *Urticaceae* are higher than the *Moraceae*, *i.e.*, they are more reduced in carpels and in perianth. The *Moraceae* are higher than the *Ulmaceae*, *i.e.*, they are more reduced in number of stamens and in perianth parts. Also, the generic relationships are indicated by this anatomical study. In the *Urticaceae*, *Laportea* and

Boehmeria are higher than *Urtica*, and *Boehmeria* is higher than *Laportea*. In *Moraceae*, *Maclura* is higher than *Morus*; and in the *Ulmaceae*, *Celtis* is higher than *Ulmus*. In the genus *Ulmus* the result of these anatomical studies places species in the same groups in which they have been placed by taxonomists. *U. americana* and *U. racemosa* come in one group, and *U. fulva*, *U. scabra*, and *U. campestris* come together in another group.

The natural position of the *Urticales* has been a debated subject. The common practice has been to place them in association with the *Amentiferae*. Jussieu, de Candolle, Endlicher, Bentham, Hooker, Engler, and Gray have assisted in establishing this arrangement. The *Amentiferae*, however, are coming to be looked upon as reduced rather than as primitive forms. Weddell (21), in 1840, associated the *Urticales* with *Tiliaceae* and *Malvaceae*, etc. One of the features that influenced him in making such a decision was the presence of "bast fibers"; but on the same feature, a relationship can be established with *Thymeliales*, which possesses several similar floral structures. Lindley (13), in 1845, placed the *Ulmaceae* singly in the *Rhamnales*. Bessey (3) and Hallier (12), in 1905, placed the *Ulmaceae*, *Moraceae*, and *Urticaceae* in the *Malvales*, as Weddell had done sixty years before. The last suggestion has received much favorable consideration from many taxonomists. The writer's anatomical studies in these suggested affinities have not progressed far enough to warrant any conclusive statement.

The floral anatomy of the species of *Ulmus* reveals a feature that should be discussed at this time, namely: the staminal cylinder as described on page 389 (Pl. XVI, figs. 16, 17, c). This may be considered homologous with the staminal tube of the *Malvaceae*. Yet, the cohesion of filaments is a character occurring in the *Parietales*, *Geraniales*, and in other small groups, and is a striking character in the *Papilionaceae*. The *Malvales*, as delimited by Engler (9), show the tendency to chorisis. Reduction, which is opposed to chorisis, is conspicuous in the *Ulmaceae*, *Moraceae*, and *Urticaceae*. However, it may be possible to accept a natural order exhibiting two such diverse processes.

There is the danger of placing the *Urticales* higher than they should be, due to the greatly reduced flower condition; the caution from Engler (10) in this regard has already been stated. Such an error can possibly be avoided by considering the characters of the order that indicate primitiveness, namely, many organs, non-cyclic condition, and preponderance of woody forms. On the other hand, zygomorphism and reduction are present in the order not as tendencies but as critical characters, *i.e.*, the characters present throughout the order. Therefore, these tendencies must be present in their nearest relatives, or were present in their immediate ancestors. It is doubtful that their ancestors were wind-pollinated. The progenitors of the *Urticales* are not in existence today. Considering their primitive characters, they are in a distinct line of descent from a protoangiospermous

plexus from which also descended the Ranalian line. The Urticales have advanced parallel with the Ranalian stock to a high degree of specialization, namely, zygomorphy. Accompanying this specialization, or following it, the Urticales show great reduction in all parts of the flower. The result has been a group of plants combining characters belonging to primitive and to recent types, a combination which makes them a generalized rather than a specialized group from which no descendants seem to have arisen.

SUMMARY AND CONCLUSIONS

1. The anatomy of the flowers of the Urticales reveals a number of features extending throughout the order, which are not appreciable from a macroscopic investigation.

a. *Ulmus*, the primitive genus, shows evidence of suppression of a whorl of stamens and of one of perianth parts. The existing stamens are fused with the gamophyllous perianth. The parts of these whorls are somewhat spiral in arrangement and very inconstant in number.

b. The bicarpellate condition has been derived from a polycarpellate condition as evidenced by the presence of vascular supply to suppressed carpels. Also, vestigial bundles indicate that the bicarpellate gynoeceum is becoming unicarpellate by the suppression of one carpel.

c. The perianth parts are reduced in number by abortion, suppression, and fusion; in some cases the inner whorl has entirely disappeared, in others vestiges of its vascular supply remain. In some forms the inner and outer whorls are fused and occur as one whorl.

d. Zygomorphy is a conspicuous character of all species studied; evidence of it is not only found externally but appears also on microscopic study of transverse sections of the flowers.

e. Palmate venation, if no longer present in the foliage, is still present in the perianth parts in some forms.

f. The ovules are foliar organs. The orthotropous ovule in the higher members of the order has come to its basal, erect position by a sinking from an apical or lateral position of the anatropous ovule in the primitive members. The "cauline" ovule in the Urticales is apparently such due to reduction. All "cauline" ovules may possibly be simply the result of the same process.

g. The vascular supply to the uniovulate ovary suggests a polyovulate ancestry.

h. Accompanying coalescence and adnation, the flowers have been greatly reduced in all floral organs.

2. In plant organs suffering reduction the vascular system disappears in advance of the organs, or persists as abortive bundles after the organs have disappeared.

3. The combination of primitive and specialized characters makes the Urticales a generalized group.

4. The Urticales are probably not far removed from primitive entomophilous ancestors.

5. Floral anatomy emphasizes the idea that the Urticales are a natural order which is made up of three natural families as classified by Engler.

6. The natural position of the Ulmaceae, Moraceae, and Urticaceae is at the culmination of a distinct line of descent from a protoangiospermous plexus from which also the Ranalian line descended.

The writer wishes to express his gratitude to Dr. A. J. Eames, to whom he is indebted for this problem as well as for advice and assistance while the work was in progress.

DEPARTMENT OF BOTANY,
COLLEGE OF AGRICULTURE,
CORNELL UNIVERSITY,
ITHACA, N. Y.

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EXPLANATION OF PLATES

The figures in the plates are greatly enlarged. The flower sections range from 0.5 mm. to 3 mm. in diameter, or 3 mm. x 5 mm. in dimension.

PLATE XV

Ulmus americana

FIG. 1. Habit sketch of flower with 8 perianth lobes and 8 stamens.

FIG. 2. Portion of perianth showing small inner lobe (*a*) and vascular supply to lobes.

FIG. 3. Longitudinal section of flower in median posterior-anterior plane. Origin of vascular supply (*b*) to perianth (*p*) and to stamens (*s*); *1*, bundle to anterior carpel; *1*¹, bundle to posterior carpel; *ov*, to placenta; *i*, to ovule in anterior carpel; *i*¹, the abortive bundle to suppressed ovule in posterior carpel; *o*¹ and *o*², placental branches passing through the inner faces of the styles; *d*⁶, abortive bundle alternating with those to the stamens.

FIG. 4. Longitudinal section of flower perpendicular to the plane of that in figure 3; *d*², *d*⁴, abortive bundles alternating with stamen bundles; *e*, abortive bundle in the carpel supply.

FIG. 5. Transverse section through pedicel; *st*, the stele.

FIGS. 6-15. Transverse sections through a flower, 40, 50, 30, and (figs. 9-15) 20 microns apart respectively. Posterior trace passes off and separates into traces to perianth lobe (*m*) and stamen (*s*). Other traces pass off successively toward the anterior side, *m*¹, *n*¹, . . . *m*⁷, *n*⁷, and each separates as does the posterior trace. Stamen trace *n*² aborts 70 microns above its origin; *d*¹ . . . *d*⁶, abortive bundles of vascular supply continuing above and alternating with that to the stamens; *c*, staminal cylinder; *t*, traces continuing into the pistil.

PLATE XVI

FIGS. 16-18. Transverse sections of flower; *m* . . . *m*⁷ and *n* . . . *n*⁷, bundles to perianth and stamens respectively. The posterior (*m*) and anterior (*m*⁷) bundles separate each into 3 strands; *1*, to posterior, *1*¹, to anterior carpel; strands *o* come together making *o* + *o* of the placental vascular system.

FIGS. 19-21. Transverse sections through upper part of pistil; *1* and *1*¹, dorsal bundles to carpels; *i*, to ovule; *i*¹, abortive bundle corresponding to *i*; *o*¹ and *o*², inner lateral bundles of styles.

FIG. 22. Section through a flower at level of stalk of pistil, an 8-merous flower.

FIG. 23. Section through a flower with 7 perianth lobes and 6 stamens.

FIG. 24. Section through a 9-merous flower.

FIG. 25. Section through a flower having a stamen (*nk*) with no accompanying perianth lobe.

PLATE XVII

Ulmus fulva

FIG. 1. Median longitudinal posterior-anterior section; supply to stamens originates some distance (6) above that to perianth; *o*, the placental strand which branches like that in *U. americana* (Pl. XV, fig. 3); *d*, abortive bundles.

FIG. 2. Transverse section through lower part of flower; *p*, perianth; *s*, stamens; *d*, abortive strands; *s*¹, abortive (lignified) strand to suppressed stamen; *t*, continuation of floral axis above the stamen supply.

Ulmus racemosa

FIG. 3. Median longitudinal posterior-anterior section of flower; *b*, origin of perianth (*p*) and stamen (*s*) strands; *o*, placental supply.

FIG. 4. Transverse section through lower part of flower; $m \dots m^7$ and $n \dots n^7$, strands to perianth and to stamens respectively; d and d^1 , abortive bundles.

Ulmus campestris

FIG. 5. Median longitudinal posterior-anterior section; bundles to stamens (s) originate above (b) those to perianth (p).

FIGS. 6, 7. Various lobing of perianth; $1 \dots 4$ are strands to main lobes; a and b , branches or separations from the main strands; s , stamen position.

Ulmus scabra

FIG. 8. Longitudinal lateral section of flower; b , space between origin of stamen and perianth bundles; x, x^2 , abortive bundles of the perianth; d , abortive bundles above those to stamens; o , the placental supply.

FIGS. 9, 10. Transverse section of flower; $m \dots m^5$ and $n \dots n^5$, bundles to perianth lobes and stamens respectively; x, x^1, x^2 , abortive bundles of perianth; d , abortive bundles alternating with stamen bundles; t , continuation of floral axis; $1, 1^1, 1^2$, dorsal bundles of 3 carpels; o , the placental supply.

PLATE XVIII

FIGS. 1, 2. Transverse sections above those of figures 9 and 10, Plate XVII; lettering the same. Perianth bundles separate into 2 to 4 strands.

Celtis occidentalis

FIG. 3. Longitudinal section of flower; b , trace from stele of pedicel which separates into perianth (p) and stamen (s) strands; o , placental supply arises or separates from anterior carpel (1^1) supply.

FIGS. 4-12. Transverse sections of flowers; in lower part of flower, stele is prominent in anterior and posterior regions; strands to anterior part of flower lead off, perianth (m) and stamen (n); $1, 1^1$, dorsal bundles of carpels; o , bundle of placental supply; o^1 and o^2 , lateral strands of the pistil.

FIG. 13. Transverse section at base of styles, o^1 and o^2 not present.

PLATE XIX

Morus alba, pistillate

1 , anterior, and 1^1 , posterior carpel bundles; p , posterior and anterior, and p^1 , lateral sepals; o , placental supply.

FIG. 1. Median longitudinal section of flower in posterior-anterior plane.

FIGS. 2, 3. Transverse section through pedicel.

FIGS. 4-9. Transverse sections of a flower; $o + o$, the union of two placental strands (as in *Ulmus*).

FIG. 10. Longitudinal section of a staminate flower; b , strand composed of stamen and perianth supply; $1, 1^1$, abortive carpel bundles.

Maclura pomifera

FIGS. 11, 12. Transverse sections through base of pistillate flower within the inflorescence axis; $1, 1^1$, anterior and posterior carpel supply; p , perianth; o , placental supply.

FIGS. 13-17. Flowers becoming distinct as well as the parts of each flower; n , abortive bundles in the perianth parts.

FIGS. 18, 19. Longitudinal median anterior-posterior section of pistillate and staminate flowers respectively.

PLATE XX

Cannabis sativa, pistillate

br , bract; s , bundle to bract; p , perianth; $1, 1^1$, traces to carpels; s , stamen; o , bundle to placenta; x , abortive bundles.

FIG. 1. Habit sketch of flower; *p*, cup-like perianth.

FIGS. 2-8. Transverse sections of flower. Origin and freeing of bract and perianth; bundles to carpels and to ovule.

Humulus Lupulus, pistillate

(Lettering as for *Cannabis*)

FIG. 9. Longitudinal median posterior-anterior section of flower.

FIGS. 10-12. Origin of bract, presence of abortive bundles.

FIGS. 13-18. Origin of perianth bundles numbered in the order of their appearance. Two carpel bundles continue into the styles.

PLATE XXI

Urtica gracilis, pistillate

1, 1', anterior and posterior carpel supplies; *o*, *o* + *o*, placental supply; *m*, posterior and anterior, and *n*, lateral perianth parts.

FIG. 1. Longitudinal median anterior-posterior section of flower.

FIG. 2. Transverse section of pedicel.

FIGS. 3-13. Transverse sections of flower; origin and the freeing of floral parts; supply to ovule.

PLATE XXII

Boehmeria cylindrica

(Lettering as for *Urtica*)

FIG. 1. Longitudinal median anterior-posterior section of pistillate flower; *o*, bundle to ovule.

FIG. 2. Transverse section of pedicel.

FIGS. 3-7. Transverse sections of pistillate flower; origin of floral organs and same becoming distinct.

FIG. 8. Transverse section of style.

FIGS. 9-13. Sections of staminate flower; 1, 1', abortive bundles to abortive pistil.

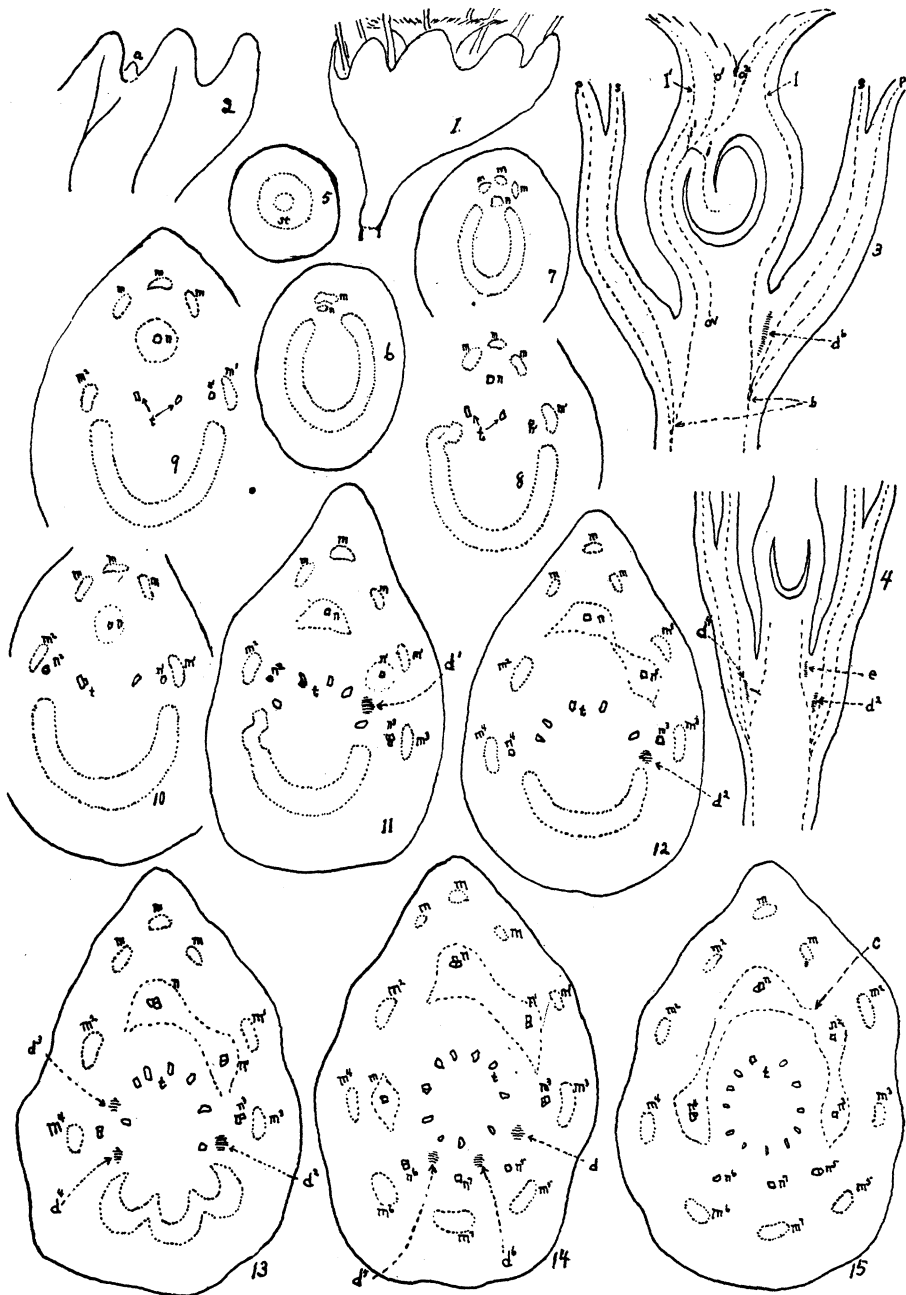
Laportea canadensis

(Lettering as for *Urtica* and *Boehmeria*)

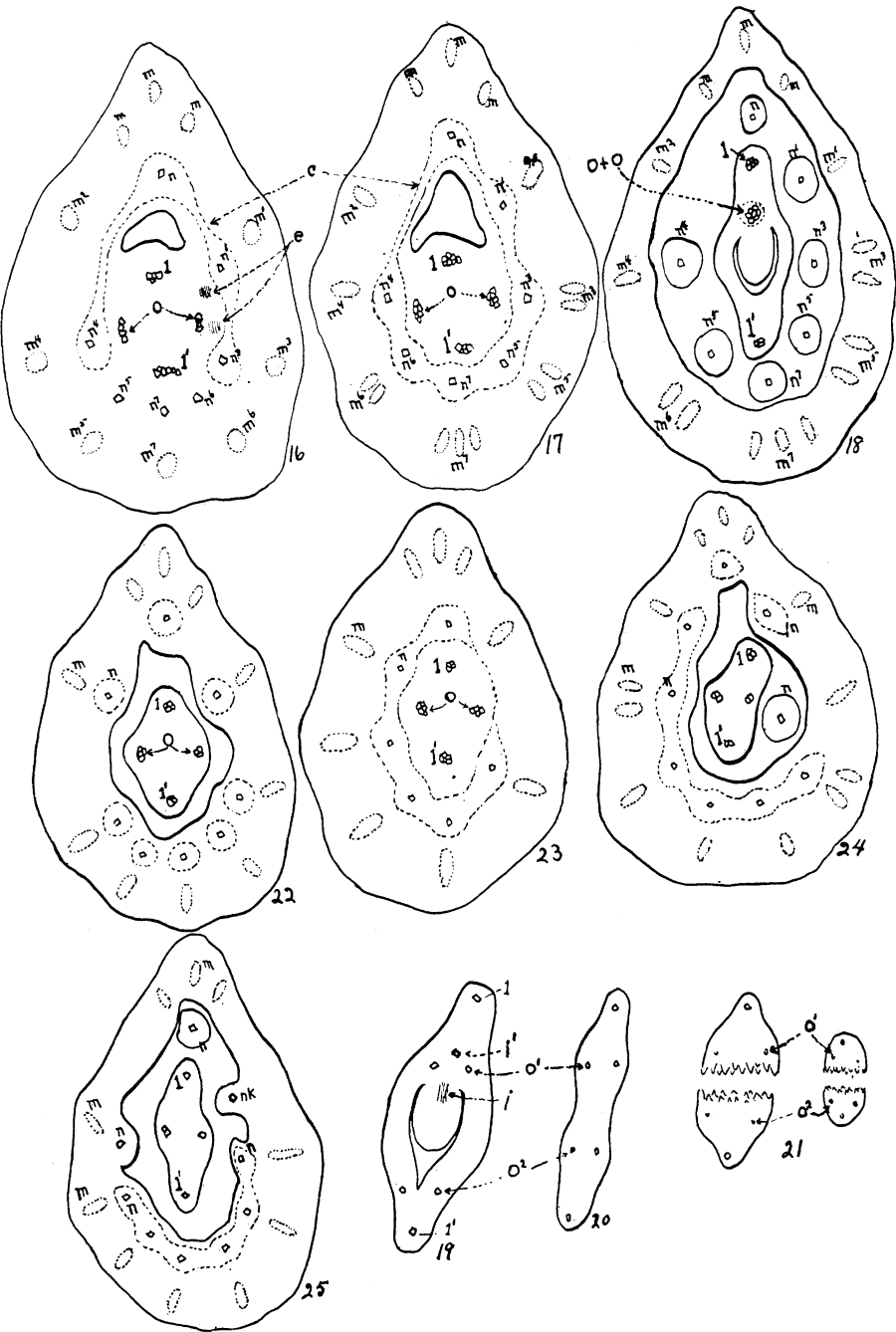
FIG. 14. Longitudinal median posterior-anterior section of pistillate flower; *f*, funiculus.

FIG. 15. Transverse section of pedicel.

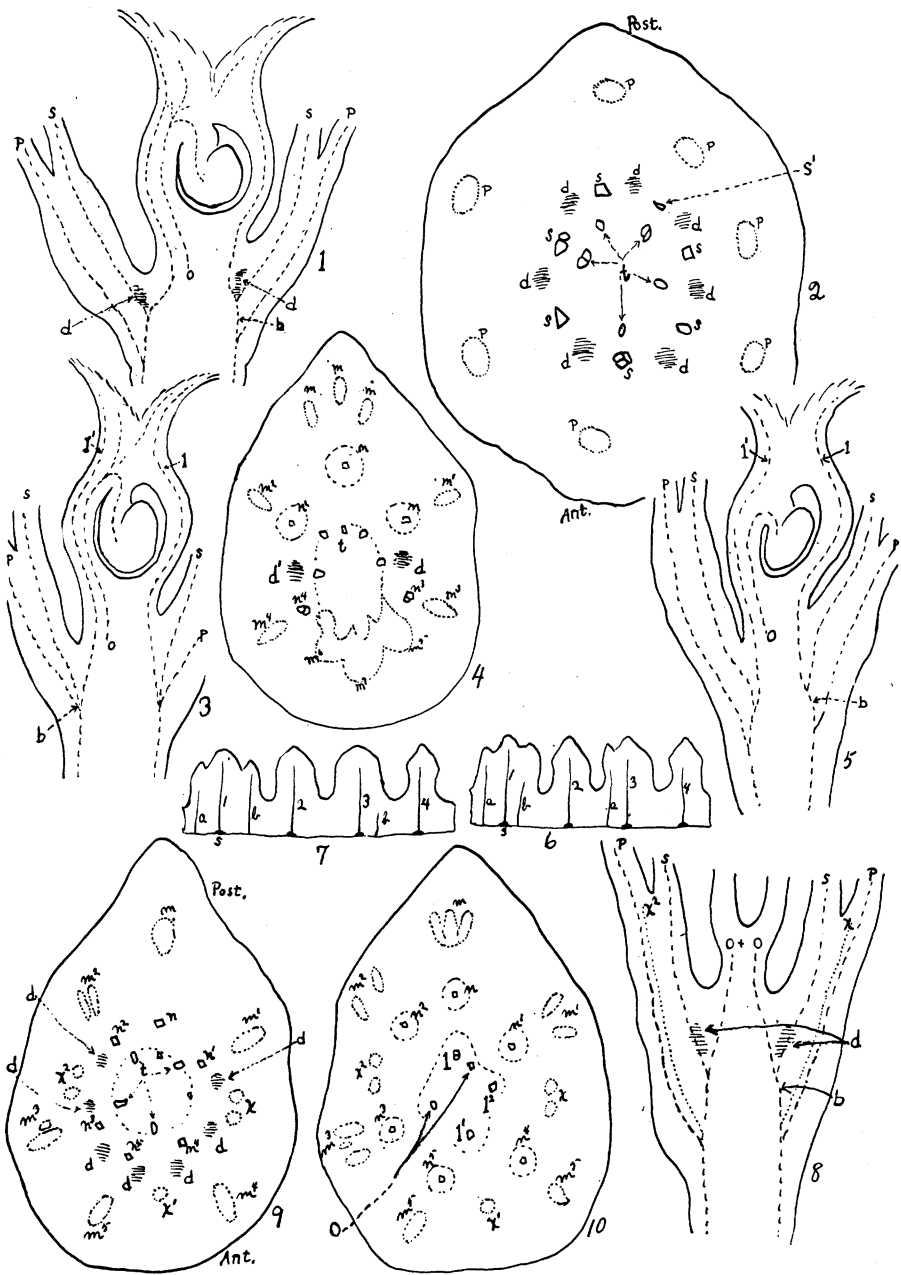
FIGS. 16-21. Transverse sections of pistillate flower; origin of floral parts and the same becoming distinct; ovule supply separating from anterior carpel supply; 1, abortive anterior carpel bundle; *m*¹, posterior sepal has its vascular supply suppressed.



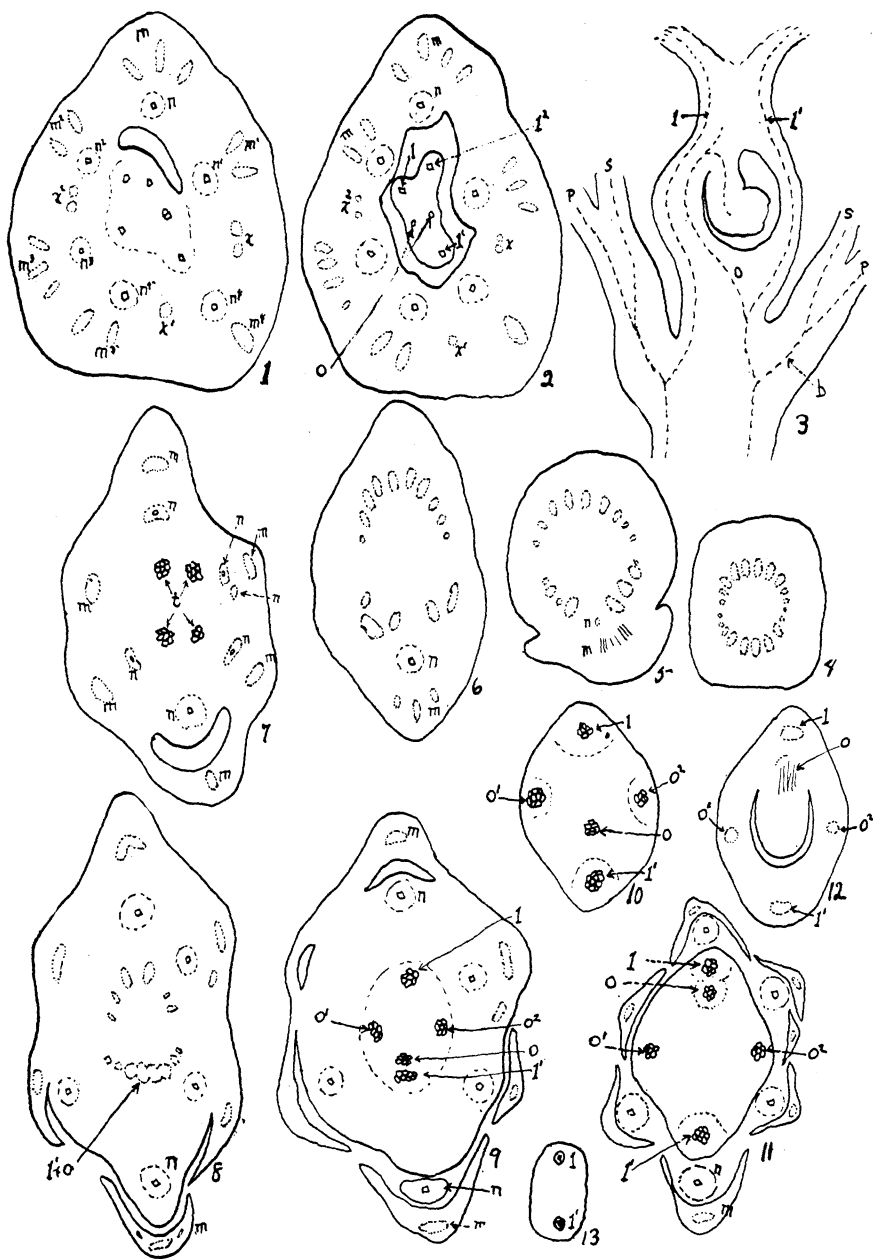
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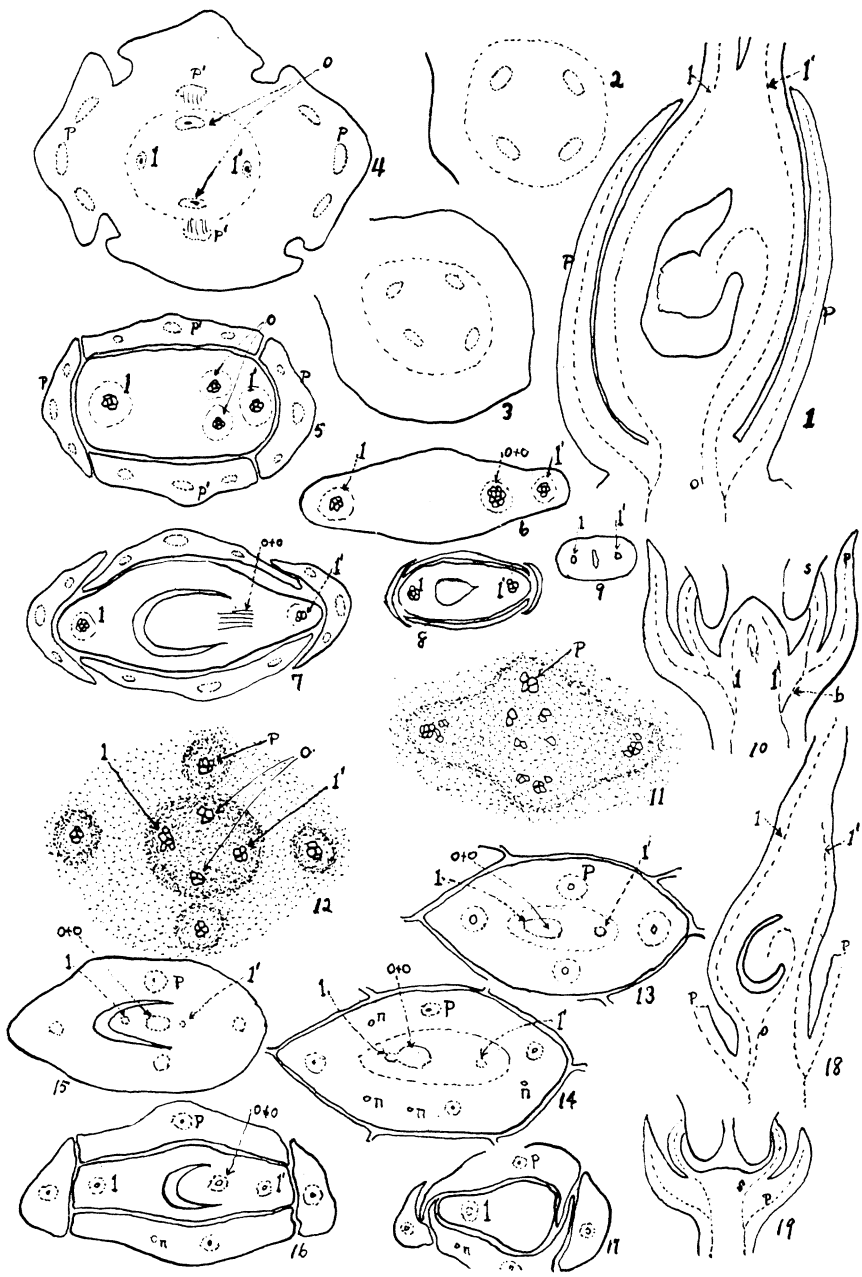
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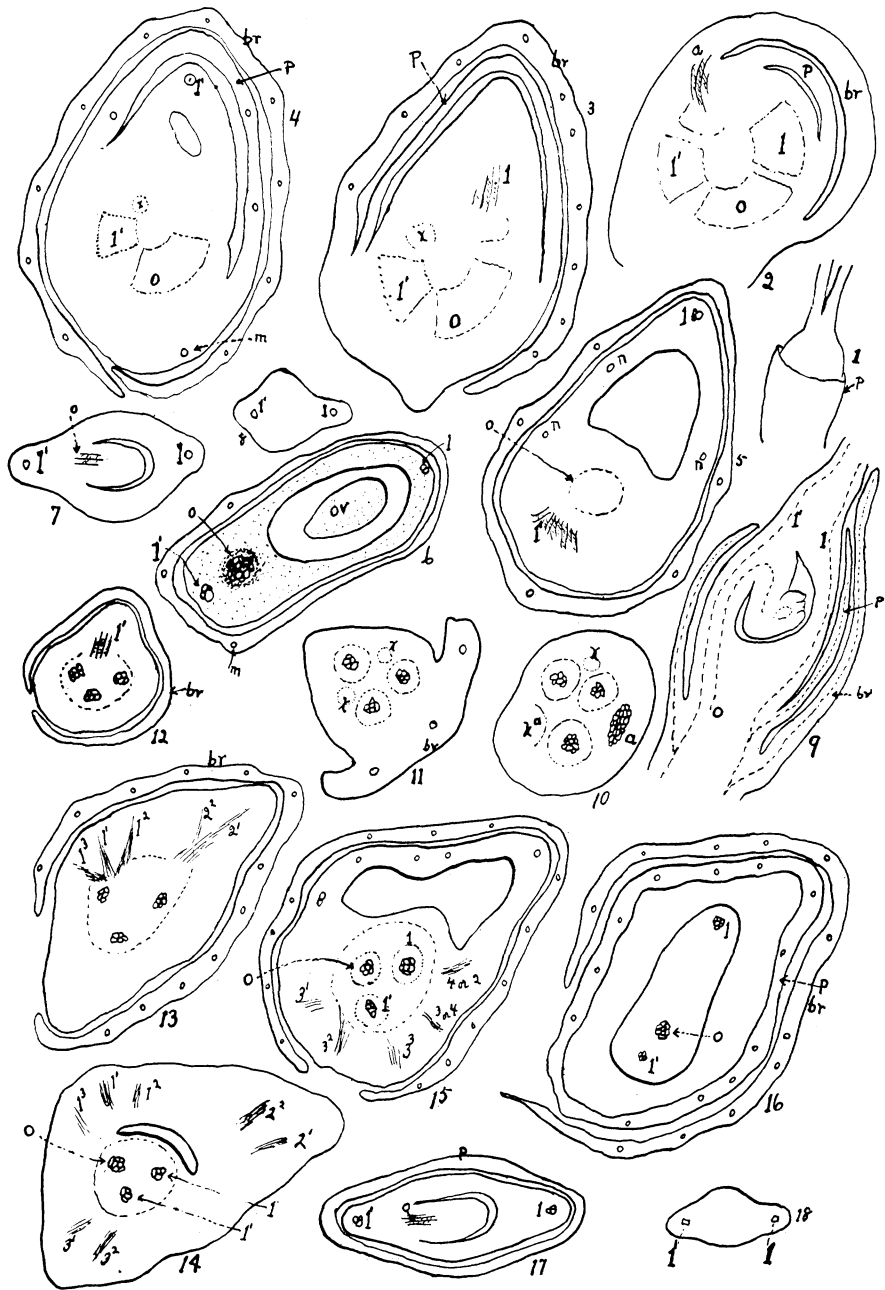
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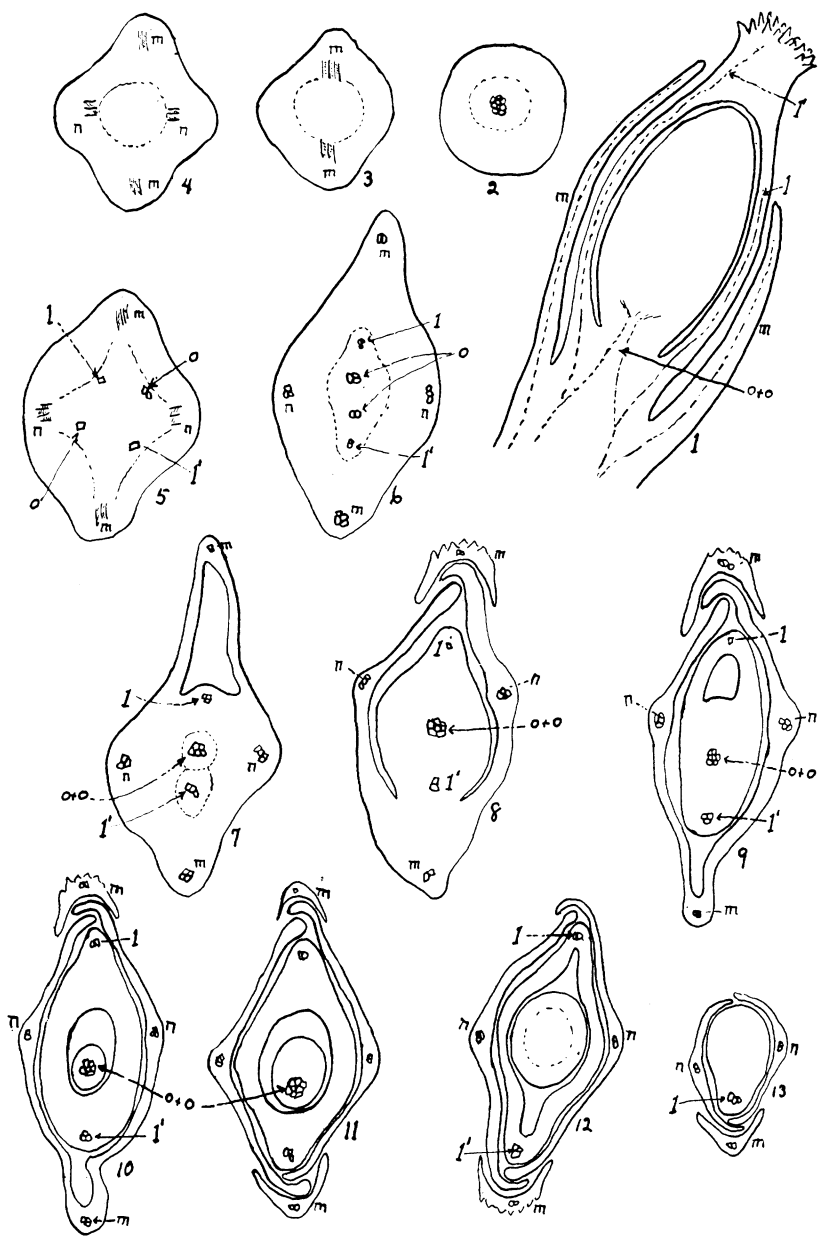
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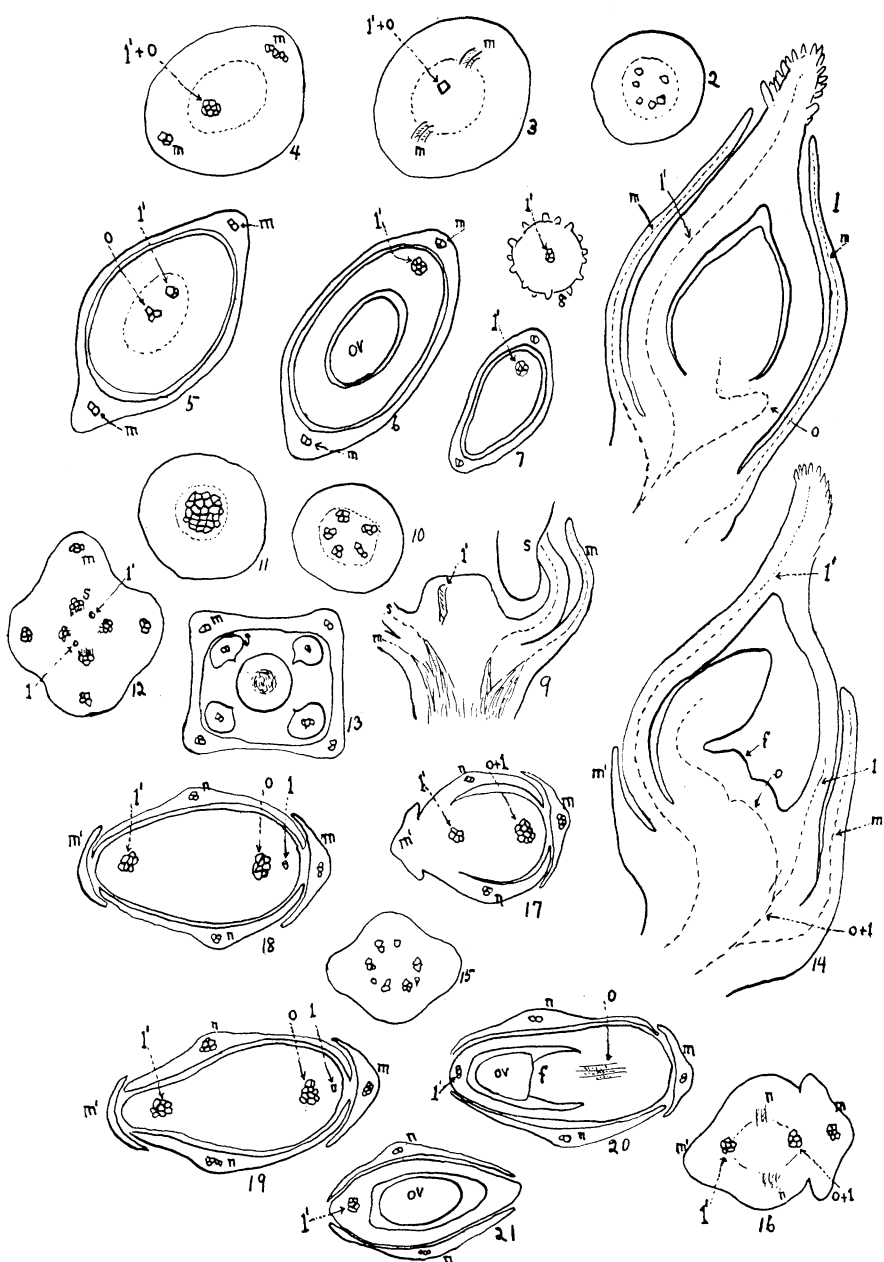
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